VARIATION OF CHELIPED ALLOMETRY IN A HERMIT CRAB: THE ROLE OF INTRODUCED PERIWINKLE SHELLS

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ABSTRACT

From Connecticut to Massachusetts, *Pagurus longicarpus* hermit crabs commonly inhabit shells of the introduced periwinkle snail, *Littorina littorea.* South of Connecticut, these periwinkles are rare and thus their shells are seldom inhabited. For male *P. longicarpus* along the Atlantic coast, use of periwinkle shells does not correlate with geographic differences in carapace length, but does correlate with geographic differences in cheliped allometry. Further, geographic patterns of shell use may indicate that periwinkle shells increased the shells available to *P. longicarpus* in New England. Such an increase in shell availability is associated with reduced relative cheliped growth in laboratory populations and may be responsible for the correlation between use of *L. littorea* shells and reduced right cheliped allometry in field populations. Museum specimens of male *P. longicarpus* from pre-*L. littorea* Connecticut also show significantly faster relative growth of the right cheliped than modern crabs.

INTRODUCTION

Empty snail shells are a critical resource for shell-living hermit crabs (Vance, 1972a; Fotheringham, 1976, Abrams, 1980; Bertness, 1981a), and hermit crab species and their inhabited shell species show a close evolutionary relationship (Jackson, 1913; Reese, 1969; Bertness, 1981b, 1982). Consequently, shells of introduced snails may affect hermit crabs dramatically (Drapkin, 1963). The European periwinkle, *Littorina littorea,* has become common along the northeast coast of North America in the last 150 years (Carlton *et al.,* 1982; Vermeij, 1982; Brenchley and Carlton, 1983; Bertness, 1984). Shells of this periwinkle are inhabited by the hermit crab *Pagurus longicarpus* in the northern part of its geographic range (see Fig. 1), and laboratory experiments suggest that these shells may have contributed to geographic variation in the morphology of *P. longicarpus* (Blackstone, 1985).

In this paper, the effects of *L. littorea* on *P. longicarpus* are elucidated by: (1) collecting data on geographic variation in carapace length, right cheliped allometry, and shell use of *P. longicarpus,* (2) correlating the morphological variation to the use of *L. littorea* shells, and (3) investigating observed associations further with modern estimations of shell availability and historical data on morphology. This study focuses on male *P. longicarpus* exclusively, since female *P. longicarpus* show less geographic variation than males and inhabit *L. littorea* shells less frequently (Blackstone, 1985).

MATERIALS AND METHODS

Geographic sampling

Collecting methods were constrained by: (1) the mobility of *P. longicarpus* (*e.g.,* Rittschof, 1980; Wilber and Herrnkind, 1982; pers. obs.), which makes quadrat sam-

pling impractical (quadrat size should encompass an average individual's territory, Southwood, 1978), and (2) the estuarine habitat of these crabs, which makes subtidal sampling with SCUBA difficult because of motorboat traffic, strong tidal currents, and high sediment loads (thus low visibility). At each site, samples were collected at low tide by areal search in the shallow subtidal, parallel to the waterline, for approximately 1 h. The smallest possible area (range 5–50 m^2) that would yield a suitable sample size (about 100 crabs) was carefully searched. The size of the sample area varied inversely with the density of the crabs.

The effectiveness of areal search as a collecting method has recently been questioned (Gilchrist and Abele, 1984). Working with four hermit crab species in the Gulf of Mexico, Gilchrist and Abele (1984) compare the population parameters obtained by different sampling methods. For *P. longicarpus,* their predation site method, employing baiting, and their transect method, employing areal search, produce samples which do not differ significantly in crab size (Fig. 1 in Gilchrist and Abele, 1984). However, these samples do differ in the degree of shell damage; *P. longicarpus* collected at simulated predation sites more frequently occupy damaged shells (Fig. 2 in Gilchrist and Abele, 1984). Because shells are usually available at predation sites, their baiting method could be attracting a biased subsample of *P. longicarpus,* comprising those individuals most highly motivated to obtain a new shell. Further, the baiting method attracts few hermit crabs off the New England coast (M. A. Shenk, pers. comm.) and thus would be inappropriate for geographic comparisons. Gilchrist and Abele (1984) recommend employing a combination of the two techniques, but for these reasons the areal search method was considered the most appropriate for this study.

The sites, dates, sizes, and regional groupings of the samples collected in 1983–1985 are shown in Table I; this study also used samples from 1980–1982 (see Blackstone, 1985). The 60-day planktonic larvae of *Pagurus* hermit crabs (Nyblade, 1974) determined the regional assignments; sites which could easily exchange larvae were grouped in the same region (see Fig. 1). Further, the high vagility of this species determined the method of statistical analysis; with high rates of migration, annual samples at the same site can be considered independent and can vary as much as simultaneous samples at different sites. Each sample was treated as a replicate sample of the *P. longicarpus* of that region. Within-region spatial and temporal variation thus is considered part of the error variation in among-region comparisons. The data justify this approach because among-region variation is much greater than within-region variation (*e.g.,* for anterior shield length, an analysis of variance with samples nested within regions yields a region effect, $F = 327$ df = 5, which is much greater than the effect of samples nested within regions, $F = 28$ df = 36).

Long Island Sound, the smallest designated region (see Fig. 1), encompasses the boundary between the rocky New England habitats where *L. littorea* abounds and the sandy estuarine habitats farther south where *L. littorea* is very rare (Vermeij, 1978). There is considerable variation in the abundance of *L. littorea* snails and shells between the north and south shores of Long Island Sound. For some analyses, Connecticut and Long Island shore samples are considered separately, though free larval exchange is likely (see Discussion).

Morphological measures

After collection each sample was preserved in 10% formalin, 90% seawater. Each crab's shell species was noted and shell length (at maximum parallel to the columellar axis) and width (at maximum perpendicular to the columellar axis) were measured

Sites, dates, sizes, and regional groupings of geographic samples[1]

Region	Site	Date	n
Northern Massachusetts	Casco Bay, ME	3 September 1985	8
	Nahant, MA	23 September 1983	112
		29 August 1985	204
	Quincy, MA	4 September 1985	78
Southern Massachusetts	Martha's Vineyard, MA	13 August 1984	133
	Charlestown, RI	14 August 1984	179
Long Island Sound	Guilford, CT	18 September 1983	157
		8 September 1984	160
	Cold Spring, NY	20 September 1983	54
		26 August 1984	92
		14 July 1985	33
		8 October 1985	38
New Jersey	Barnegat Bay, NJ	4 September 1983	79
		20 August 1984	59
		16 September 1985	57
	Corson's Inlet, NJ	16 September 1984	306
Virginia	Chinoteague, VA	19 September 1984	135
	Cherrystone, VA	20 September 1984	97
	Oregon Inlet, NC	22 September 1984	14
Carolinas	Beaufort, NC	25 September 1984	170
	Topsail Inlet, NC	26 September 1984	93
	Southport, NC	27 September 1984	102
	Murrell's Inlet, SC	28 September 1984	115
	Folly Beach, SC	30 September 1984	28

[1] Samples from 1980–1982 are described in Blackstone (1985) and have been deposited in the collections of the Division of Invertebrate Zoology, Yale Peabody Museum, nos. 8120–8137. Samples from 1983–1985 have been deposited in the collections of the Academy of Natural Sciences of Philadelphia, nos. CA4566–CA4584. All sample regions and sites from 1980–1985 are shown in Figure 1; note that not all sites are from the states used to designate the regions.

with a vernier caliper. A categorical index of shell height was calculated by shell length/width (0 = low-spired, ratio less than 1.5; 1 = high-spired, ratio greater than 1.5; this is a somewhat arbitrary designation, but it separates the shells used by *P. longicarpus* in the study areas into recognizably low-spired and high-spired species, see Blackstone, 1985, and spire height is related to shell preference, see below). A categorical index of shell fit was also noted (0 = shell fit adequate to protect crab, crab able to retract fully and form an operculum with its chelae, or 1 = shell fit inadequate because of small size or structural damage, crab unable to fully retract). Clear determination of this index was possible in almost all cases because *P. longicarpus* preserved in 10% formalin die retracted fully into their shells (unless the shell was so small that retraction was impossible). The few individuals intermediate in shell fit were excluded from further analysis. If possible the crab was removed from its shell by gently pulling its appendages; usually removal was not possible and the shell was cracked in a small vice. The crab was sexed by pleopodal morphology. The hard part of the carapace (anterior shield length, Fig. 2) was measured using a dissecting microscope equipped with an ocular micrometer. The total length of the right cheliped (Fig. 2) was then measured with a vernier caliper unless this appendage had been recently regenerated. (A recently regenerated cheliped is much shorter than the pereiopods and has an atypical color.) For some of the earlier samples, right chela length
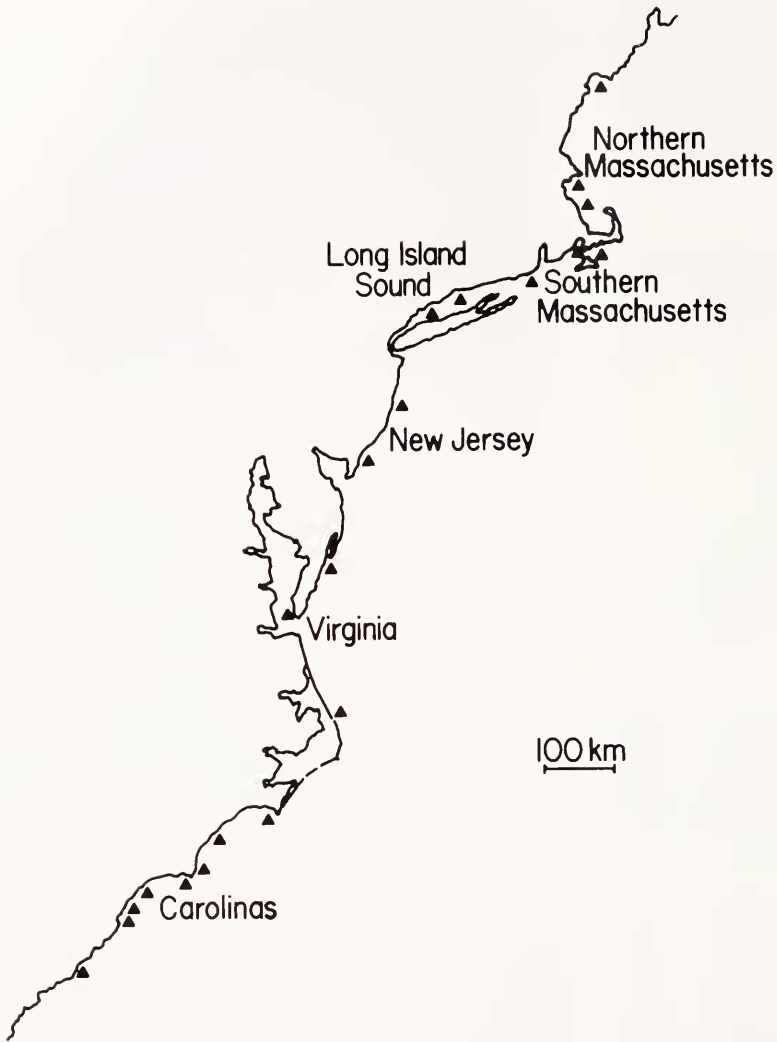
FIGURE 1. The Atlantic coast of North America from Maine (approx. 70° W. lat., 44° N. long.) to Georgia (approx. 80° W. lat., 33° N. long.) showing the regions and sites sampled. Sites (triangles) include those from 1980–1982 (see Blackstone, 1985) and 1983–1985 (Table I). Rocky substrata and periwinkle snails are common northward from the northern shore of Long Island Sound. Primarily sandy substrata from Long Island southward to Virginia support few periwinkles; south of Virginia periwinkles do not occur.

instead of cheliped length was measured. This measure shows the same pattern as right cheliped length (Blackstone, 1985), and only the cheliped data are presented.

Anterior shield length is a measure of carapace and cephalothorax size in *P. longi-carpus*. Since anterior shield lengths show slightly non-normal distributions and correlations between sample means and variances, a natural logarithmic transformation was done to better meet the assumptions of analysis of variance. Cheliped allometry was measured by double logarithmic, least-squared regressions of right cheliped
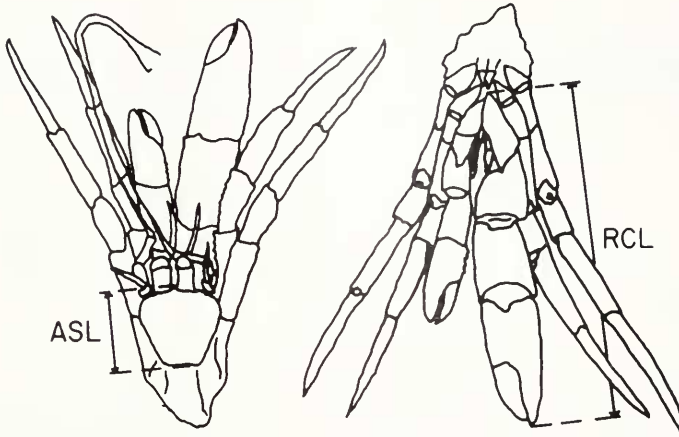
FIGURE 2. Camera lucida tracings of the calcified parts of a *Pagurus longicarpus* hermit crab. Anterior shield length (ASL) is shown on the dorsal tracing, while right cheliped length (RCL) is shown on the ventral tracing.

length on anterior shield length. The high correlation coefficients obtained indicate that other bivariate linear methods would yield similar results (Yates, 1950; Gould, 1966; Rayner, 1985). The slope of these regressions represents the relationship between the specific growth rates of the two parts (Huxley, 1932; Teissier, 1960; Laird, 1965; Shea, 1985). If this slope is greater than unity, the right cheliped has a faster specific growth rate than the anterior shield. Differences among regions were tested using analysis of covariance tests for homogeneity of slopes.

Estimating shell availability

Samples of empty shells not only are rarely obtainable, but cannot be used to measure shell availability with certainty (Wilber and Herrnkind, 1982; Blackstone and Joslyn, 1984). Abundances of living gastropods have different implications depending on the ecological circumstances (Spight, 1977; Wilber and Herrnkind, 1982). Here, data on shell use provide insight into shell availability as perceived by *P. longicarpus*. Observed shell use reflects perceived shell availability, shell preference, and ecological factors (Reese, 1962, 1969; Young, 1979). Studies of the shell preferences of *P. longicarpus* (Mitchell, 1975; Blackstone, 1984; Blackstone and Joslyn, 1984) indicate: (1) preferences for shells that provide adequate fit (defined above), and (2) preferences for high-spired shells (defined above) at small sizes and low-spired shells at larger sizes (greater than 3.3 mm anterior shield length). Patterns of shell use from geographic samples may thus be interpreted; if a crab occupied a shell which is not of the preferred fit or shape, that crab likely perceived a deficiency in the available shell resource. Ecological factors will affect estimates based on shell fit, since hermit crabs in ill-fitting shells are more susceptible to predators and other agents of mortality (Reese, 1969; Vance, 1972b). Estimates based on shell shape should be less affected by ecological factors. Because hermit crabs switch shells frequently, these measures of perceived shell availability must be made at a populational level. Also, this method implies that shell preference is relatively constant in geographic populations of *P. longicarpus;* while available data largely support this interpretation (Blackstone, 1984), this question could be investigated further.

TABLE II

Regional differences in anterior shield length, cheliped allometry, and use
of Littorina littorea shells in male Pagurus longicarpus

| | Shield length | | | Cheliped allometry[1] | | | | L. littorea |
Region	Mean	SD	(n)	Slope	SE	r^2	(n)	Inhabited
Carolinas	2.50	0.61	(584)	1.32	0.02	0.96	(269)	0%
Virginia	3.14	0.54	(113)	1.34	0.03	0.95	(98)	0%
New Jersey	4.22	0.82	(420)	1.29	0.02	0.93	(258)	5%
Long Island Sound	2.96	0.72	(1087)	1.26	0.02	0.93	(448)	27%
Southern Massachusetts	3.77	0.94	(219)	1.21	0.02	0.96	(139)	79%
Northern Massachusetts	4.88	1.39	(509)	1.21	0.01	0.97	(346)	62%

[1] Linear regression of the natural logarithm of the right cheliped length on the natural logarithm of the anterior shield length. Regression slope, standard error of slope, correlation coefficient, and sample size are shown. (Sample sizes for cheliped allometry are smaller than those for shield length; many crabs from all samples had missing or regenerate chelipeds; also some early samples were measured for right chela, rather than cheliped, length.)

RESULTS

Morphological variation

There is significant among-region variation in anterior shield length in male *P. longicarpus* (ANOVA, F = 327, df = 5, *P* < .0001), but this variation does not correlate with the use of *L. littorea* shells (Table II). For instance, in New Jersey, *P. longicarpus* are large, but inhabit few *L. littorea* shells. On the other hand, the cheliped allometry of male *P. longicarpus* shows an inverse correlation with the use of *L. littorea* shells (Table II). In regions where *L. littorea* is rare (Carolina, Virginia, New Jersey), the right cheliped grows significantly faster relative to the anterior shield than in regions where *L. littorea* is commonly used (Massachusetts) (ANCOVA, P < .01).

In Long Island Sound there are within-region differences in the abundance of periwinkle snails and their shells. On the northeast (Connecticut) shore, periwinkles are abundant on the primarily rocky substrata, while on the southwest (Long Island) shore, periwinkles are scarce on the primarily sandy substrata (Vermeij, 1978). A comparison of sites from these two shores (Fig. 3) also shows an inverse correlation
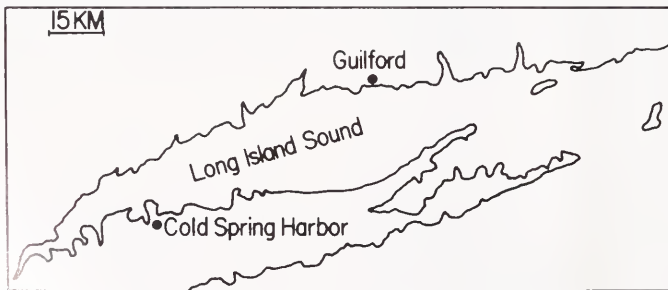

FIGURE 3. Long Island Sound showing the two sites sampled. The northeast Connecticut shore (Guilford) is primarily rocky substrata and periwinkle snails are abundant, while the southwest Long Island shore (Cold Spring Harbor) is primarily sandy substrata and periwinkles are rare.

TABLE III

Micro-geographic and historical differences in cheliped allometry and use of Littorina littorea *shells for male* Pagurus longicarpus *from Long Island Sound*

	Cheliped allometry[1]				L. littorea Inhabited
	Slope	SE	r^2	(n)	
Guilford, Connecticut	1.21	0.02	0.92	(358)	32%
Cold Spring, Long Island	1.38	0.06	0.86	(90)	5%
Long Island Sound (1873)	1.32	0.05	0.91	(72)	0%

[1] As in Table II.

between relative growth and the use of periwinkle shells (Table III). Guilford, Connecticut, crabs differ significantly from Cold Spring Harbor, Long Island, crabs both in relative cheliped growth ($P = 0.009$, ANCOVA test for homogeneity of slopes) and in use of *L. littorea* shells (*L. littorea*: native shells, 286: 618, 10: 173, Guilford and Cold Spring respectively; G-test of independence = 66.7, df = 1, $P < 0.0001$).

The observed relationship between reduced relative growth and use of *L. littorea* shells prompted a search for pre-*L. littorea* historical samples of *P. longicarpus* (see Appendix). The only such sample large enough to be useful was from Long Island Sound (exact location unknown). The relative cheliped growth of the pre-*L. littorea* males from Long Island Sound is not significantly different from that of modern males from Long Island, New Jersey, and more southern regions (ANCOVA, $P > .25$). However, these pre-*L. littorea* males show faster relative cheliped growth than Connecticut or Massachusetts males (Table III; ANCOVA, $P < .05$).

Estimates of shell availability

The low-spired shells of adult periwinkles are intermediate in size between those of the small native snails (*Ilyanassa, Nassarius, Urosalpinx*) and large native snails (*Polinices*) (Fig. 1 in Blackstone, 1985). Further, periwinkles may have reduced the abundance of the small, high-spired native mud snails (*Ilyanassa* and *Nassarius*) either by direct competition (Brenchley and Carlton, 1983) or by habitat alterations (Bertness, 1984). In areas where periwinkles are abundant, it is expected *a priori* that (1) medium-size, low-spired shells are more abundant, and (2) small, high-spired shells are less abundant.

The results of estimates of shell availability largely confirm these expectations (Fig. 4). Small male *P. longicarpus* (less than 3.3 mm anterior shield length) always inhabit shells which fit, but in regions where periwinkle shells are abundant (Connecticut and Massachusetts), they often inhabit low-spired shells, the less preferred shape at these sizes (Mitchell, 1975; Blackstone, 1984; Blackstone and Joslyn, 1984). This suggests that the availability of small, high-spired shells is lower in New England than in southern regions.

Shell availability estimates for medium-size male *P. longicarpus* (anterior shield length 3.3–4.9 mm) also show geographic variation. In the Carolinas and Virginia these crabs all inhabit shells which fit, but more than half inhabit high-spired shells, the less preferred shape at these sizes (Mitchell, 1975). In these regions, the low-spired shells of the large native littorine, *Littorina irrorata,* are an important component of the preferred shell resource, while *L. littorea* shells do not occur or are very rare.
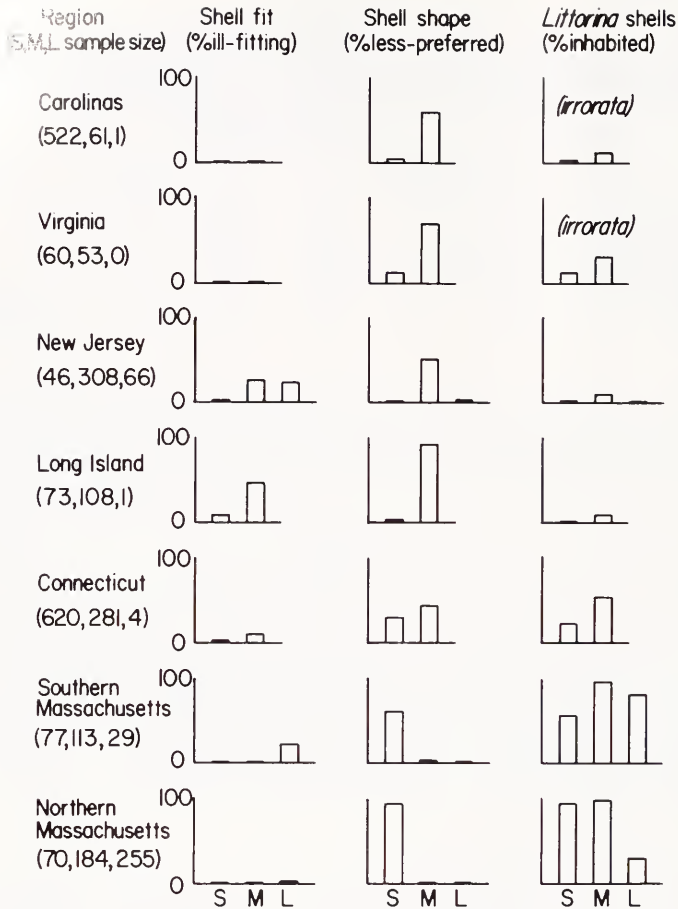
FIGURE 4. For six geographic regions (Long Island Sound is divided into Long Island and Connecticut, see Fig. 3), indices of shell fit and shell shape provide estimates of shell availability and the impact of *Littorina littorea* shells on small (S; less than 3.3 mm anterior shield length), medium (M; between 3.3 and 4.9 mm ASL), and large (L; greater than 4.9 mm ASL) *Pagurus longicarpus* males. In the Carolinas and Virginia, shells of *Littorina irrorata* (plotted), a native snail, are an important part of the shell resource, but many medium-size crabs inhabit shells of the less preferred shape. In New Jersey and Long Island, *L. irrorata* is very rare or does not occur and *L. littorea* (plotted) is also rare; many medium-size crabs inhabit shells which do not fit and many inhabit shells of the less-preferred shape. In New England (Connecticut and Massachusetts), hard substrata and *L. littorea* (plotted) are common and: (1) more medium-size crabs inhabit shells which fit than in New Jersey and Long Island (G-tests, $P < .001$), (2) fewer medium-size crabs inhabit shells of the less-preferred shape than in Long Island and more southern regions (G-tests, $P < .001$), and (3) more small crabs inhabit shells of the less-preferred shape than in Long Island and more southern regions (G-tests, $P < .001$). (Samples sizes <5 are not plotted.)

In New Jersey and Long Island, many medium-size specimens of *P. longicarpus* occupy shells of less than preferred fit or shape. *Littorina irrorata* shells are very rare or do not occur in these areas (Vermeij, 1978), while *L. littorea* shells are inhabited by 8% of the medium-sized crabs (Fig. 4). On the Connecticut shore of Long Island Sound, significantly more *L. littorea* shells are occupied by medium-size crabs (52%, G-test, $P < .0001$), and both indices of shell fit and shell shape indicate that preferred

shells are more available to medium-size crabs in this area than in southern Long Island Sound and New Jersey.

In Massachusetts, virtually all medium-size specimens of *P. longicarpus* occupy *L. littorea* shells and very few crabs occupy less than preferred shells. Even in northern Massachusetts where large, low-spired shells of native *Polinices* species are occupied by many large males (>4.9 mm anterior shield length; Fig. 4), medium-size crabs occupy *L. littorea* shells almost exclusively (97%, Fig. 4).

DISCUSSION

The introduction of *L. littorea* and the subsequent availability of its medium-size, low-spired shells may have significantly improved shell availability as perceived by medium-size male *P. longicarpus* specimens in New England. A discontinuity in the native shell resource is apparent between small and large species of shells (Blackstone, 1985). Medium-size crabs are most likely to perceive this discontinuity. Indices of perceived shell availability calculated for these crabs suggest that the introduced periwinkle shells improve shell availability for this size class. While one index (shell fit) could easily be influenced by ecological factors, the other (shell shape) is much less sensitive. Both indices suggest that medium-size male *P. longicarpus* perceive shell availability as high only in areas where *L. littorea* shells are very common. Again, geographic variation in shell preference could affect this conclusion, but available data (Mitchell, 1975; Blackstone, 1984) suggest that shell preference is rather constant in *P. longicarpus* along the Atlantic coast.

Reduced shell availability, or more precisely, an increased incidence of ill-fitting shells in a hermit crab population, is associated with increased cheliped allometry. Laboratory experiments suggest that *P. longicarpus* specimens which inhabit shells of an inadequate fit tend to exhibit faster relative growth of the right cheliped than those which inhabit shells of adequate fit (Blackstone, 1985, 1986). The observed geographic pattern of cheliped allometry thus may be related to the data on shell fit.

In the Carolinas and Virginia, *P. longicarpus* males exhibit a high rate of relative cheliped growth but do not inhabit shells of inadequate fit. While the shell shape index suggests that medium-sized crabs perceive deficiencies in the shell resource, ecological factors might prevent crabs in ill-fitting shells from remaining in the population. Populational samples do not contain crabs which experienced ill-fitting shells, and such samples will not show environmentally induced acceleration of relative growth. The high rate of cheliped allometry in these regions probably stems from genetic factors, and laboratory experiments support this interpretation (Blackstone, 1985, in press).

In New Jersey and Long Island, *P. longicarpus* males exhibit a high rate of relative cheliped growth and also inhabit shells of inadequate fit. Populational samples include many crabs which experienced ill-fitting shells (measures of shell fit are best interpreted at the population level, since these crabs switch shells frequently). The high rate of cheliped allometry in these areas may stem from environmentally induced acceleration of relative growth.

In Connecticut and Massachusetts, *P. longicarpus* males exhibit a low rate of relative cheliped growth and seldom inhabit shells of inadequate fit. Data from Long Island Sound suggest that this low rate of cheliped allometry may stem from the introduction and use of periwinkle shells.

In Long Island Sound, *P. longicarpus* are probably homogeneous for genetic factors controlling cheliped growth, because hydrographic patterns indicate that planktonic larvae should be well dispersed (see Riley *et al.,* 1959). While strong selection

could override this gene flow (*e.g.,* Koehn *et al.,* 1976), there is no evidence that strong selection for slight differences in cheliped proportion is operating. Nevertheless, *P. longicarpus* males from the Connecticut shore show reduced relative cheliped growth when compared to those from the Long Island shore and this difference is associated with the use of *L. littorea* shells (Table III). Further, the relative cheliped growth of males from a pre-*L. littorea* Long Island Sound sample is greater than that of modern males from Connecticut, but equal to that of males from Long Island.

Of the possible explanations for these geographic and historical patterns, the most parsimonious one, given the available data, is that the introduction of *L. littorea* increased the shell availability as perceived by male *P. longicarpus* in some northern areas where it became common (Connecticut and Massachusetts), but not in other northern areas where it is still scarce (Long Island and New Jersey). In areas where shell availability was increased, fewer crabs inhabited ill-fitting shells and cheliped allometry decreased. These results may indicate that historical change in allometry can be ecophenotypic. This supports suggestions made by other workers (Fryer *et al.,* 1983, 1985; Kat and Davis, 1983; Kemp and Bertness, 1984; Palmer, 1985).

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APPENDIX

Curators of the following museums provided information on historical collections of *P. longicarpus:* U. S. National Museum of Natural History (Washington), Academy of Natural Sciences (Philadelphia), American Museum of Natural History (New York), Yale Peabody Museum (New Haven), Museum of Comparative Zoology (Cambridge), and British Museum, Natural History (London).

Pre-*L. littorea* specimens of *P. longicarpus* were located for Massachusetts

(n = 144) and Long Island (n = 321). Most of the specimens were retracted inside their occupied shells and could not be measured. Thus populational measures (*e.g.,* mean anterior shield length) were impossible. The maximum anterior shield length of specimens out of shells was similar to that found in modern samples (historical: modern; for Long Island Sound, 5.3:6.1 mm; for Massachusetts, 7.7:8.3 mm). This suggests that *P. longicarpus* did not increase in size, particularly when differences in sample sizes are considered (historical:modern; sample sizes for Long Island Sound, 321:1807; for Massachusetts, 144:1060). The shells inhabited by these pre-*L. littorea* hermit crabs are the same as the native species new inhabited.

Measures of cheliped allometry could be taken. These are presented for 72 male crabs from an 1873 Long Island Sound sample (YPM #7935; *L. littorea* arrived in Long Island Sound after 1875; Carlton *et al.,* 1982; Vermeij, 1982; Brenchley and Carlton, 1983). This is the only historical sample with many (>15) specimens out of shells.